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RESEARCH ARTICLE

Spatial and temporal patterns of fish assemblages in Lake Nokoué and the Porto-Novo Lagoon (Benin, West Africa)

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Abstract. Fish distribution in the lagoon complex of Lake Nokoué and Porto-Novo Lagoon is poorly documented. The lagoon complex is of particular interest because of its contribution to the local supply of animal protein. The fish communities in the complex were studied monthly between January and December 2015 at six sampling sites using two sets of gillnets with varying mesh sizes. The study applied a non-linear self-organizing map (SOM) method to classify the sampling sites based on the composition of fish assemblages, and an index of indicator value (IndVal) was calculated for each species identified. In total, 58 species from 49 genera and 34 families were cataloged with 45 species observed in Lake Nokoué and 48 in the Porto-Novo Lagoon. Notably, 35 species were common to both water bodies. The analysis revealed a dominance of occasional continental (20.7%) and strict estuarine species (20.7%). The SOM analysis suggested a tripartite structure of the fish communities, largely influenced by the geographical positioning of the sampling sites. The IndVal method identified 28 indicator species in the typical assemblages delineated by the SOM approach. The study highlights the importance of these indicator species for the conservation efforts aimed at sustaining the ichthyofauna of the lagoon complex.

Keywords: artificial neural networks, coastal river, fish communities, indicator value method, Ouémé River

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Introduction

Lagoons are ecosystems of immense biodiversity that provide irreplaceable habitats, spawning grounds, and nurseries for numerous species (Ruiz et al. 2006). Their significance to both ecology and the human economy is increasingly recognized (Ould Mohamedou et al. 2008). In Benin, inland fisheries account for approximately 75% of the country's fish production and nearly 31% of its consumption of animal protein (Lalèyè 1995). The lagoon complex, encompassing Lake Nokoué and the Porto-Novo Lagoon and classified as a part of Ramsar site 1018, stands out as Benin's most significant continental water body in terms of size (180 km^2), productivity, and utilization (Lalèyè 1995, Lederoun et al. 2018). This system alone contributes between 65 and 70% to the country's continental water fisheries production. However, the increase in commercial fishing since the 1990s has led to a gradual decline in fish populations from overfishing (Lederoun et al. 2020). While studies focusing on population dynamics and sustainable management practices have been conducted for certain target species (*Coptodon guineensis* (Günther), *Hemichromis fasciatus* Peters, *Sarotherodon melanotheron* (Rüppell) (Niyonkuru 2007, Niyonkuru et al. 2007, Lederoun et al. 2020), comprehensive research on the fish ecology within this complex remains scarce. Previous studies on the spatio-temporal variations of the ichthyofauna are outdated, with the most recent data dating back over two decades (Adité and Thielen 1995, Lalèyè et al. 2003, 2004, Villanueva 2004). Given this context, it is imperative to update our understanding of the fish fauna in this lagoon complex, to monitor ecological changes over time, and to inform conservation efforts more effectively.

This study aims to catalog the diversity of fish species in the lagoon complex, examine their spatio-temporal patterns, and identify indicator species within the observed ichthyological communities, thereby contributing to the preservation and sustainable management of this vital ecological and economic resource.

Materials and methods

Study area

The study was conducted in the southeastern part of the Benin lagoon network, focusing on the interconnected Lake Nokoué and Porto-Novo Lagoon complex. Lake Nokoué (Fig. 1) spans an area of 150 km^2 and is located between 6°20’ and 6°30’ North latitude and 2°20’ and 2°35’ East longitude. It is the largest water body in Benin (Lalèyè 1995, Niyonkuru 2001, Niyonkuru and Lalèyè 2010, Lederoun et al. 2020), with an average depth of 2.2 m and a maximum depth of 4.1 m, extending 20 km east-west and 11 km north-south. The lake receives freshwater inflows from the Ouémé and Sô rivers and is connected to the

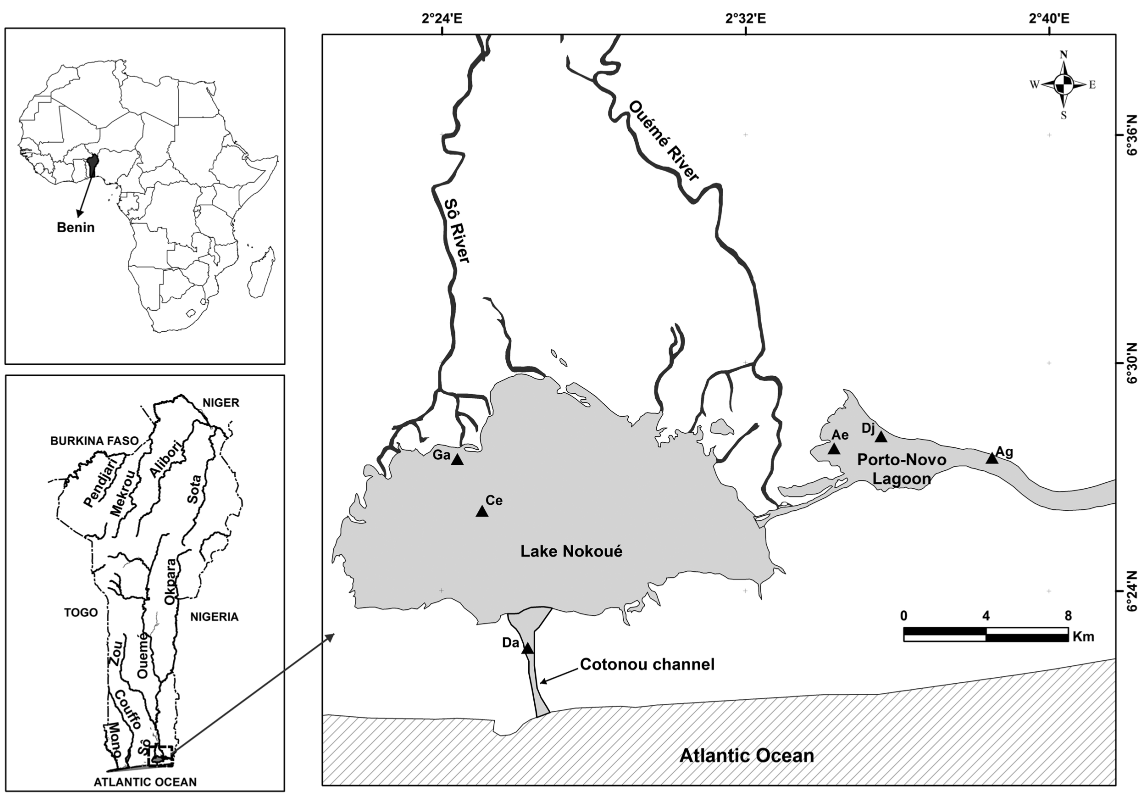


Figure 1. Study area, showing sampling sites (▲). Ae – Aguégués; Ag – Agbokou; Ce – center of Lake Nokoué; Da – Dantokpa; Dj – Djassin; Ga – Ganvié.

Porto-Novo Lagoon (Fig. 1) via the Totchè Canal (Lalèyè 1995, Niyonkuru and Lalèyè 2010, Lederoun et al. 2018). Additionally, it is influenced by wastewater from Abomey-Calavi, stormwater from Cotonou, and seawater through the Cotonou Channel (Mama 2010). The Porto-Novo Lagoon, covers an area of 30 km^2 and is located between 6°25' and 6°30' North latitude and 2°30' and 2°38 East longitude. This lagoon, narrower than Lake Nokoué, measures 7 km in length and 4 km in width, with an average depth of 1.3 m. It serves as the final conduit for the Ouémé River waters to the ocean via the Lagos Channel.

Its geographical location means the lagoon system is characterized by a transitional subequatorial climate, marked by two rainy seasons and two dry seasons: a long dry season (from mid-November to the end of March), a long rainy season (from early April to mid-July), a short dry season (from mid-July to mid-September), and a short rainy season (from mid-September to mid-November). This climatic pattern plays a crucial role in the ecological dynamics and biodiversity of the region (Niyonkuru and Lalèyè 2010, Lederoun et al. 2018, 2020).

Fish sampling

Data were collected monthly throughout 2015 from January to December with two sets of five gillnets, each of which was 30 m long and 1.5 m deep with 10, 12, 17, 20, and 22 mm mesh sizes. This selective sampling approach, when applied consistently, facilitated the acquisition of comparative data on the fraction of the fish population that is susceptible to capture (Da Costa et al. 2000, Lederoun 2015, Lederoun et al. 2021). Only night fishing was conducted (Lederoun et al. 2021). Each sampling site underwent two nights of fishing per month, totaling 12 nights per sampling effort. Nets were set at dusk, between 17:00 and 18:00, and retrieved the following morning, between 06:00 and 07:00. The procedure was repeated on consecutive nights to maximize the breadth of data collected. The catches of each net were processed separately. For this purpose, an inventory of species was made on site; unidentified species were encoded to be preserved in 10% formalin for confirmation of identification in the laboratory according to Paugy et al. (2003a, 2003b).

Data analysis

First, we established a list of the species collected from the various sites. The taxonomic order of families followed Nelson et al. (2016), while genera and species were arranged alphabetically. The frequency of occurrence of a species was calculated as follows:

$$F= F_i\, x100/F_t$$

Fi = number of surveys containing species *i*; *Ft* = total number of surveys conducted.

Three groups of species were identified based on the value of *F* (Dajoz 1982): (1) constant species ($F >$ 50%), (2) accessory species (25% < F < 50%), and (3) accidental species (F < 25%). Simultaneously with the assessment of the occurrence of each species, the degree of similarity among sites was also calculated. The Jaccard similarity index was calculated using Past 4.09 (Palaeontological Statistics Software).

Temporal and spatial variations in species richness, the Shannon-Wiener diversity index, and the Pielou equitability index were analyzed and illustrated. Specific richness was the number of species represented in the community. The Shannon diversity index was calculated for each site and month according to the following formula (Dajoz 1982):

$$H' = -\Sigma\, [Pi\ log2\ (Pi)]$$

where H' is Shannon diversity index, Pi = N i / N, Ni is the number of individuals representing species i, and N is the total number of individuals.

The value of H' is generally between 1 and 4.5 or exceptionally higher in the case of large samples of complex communities.

Equitability E' was calculated using the following formula (Dajoz 1982):

$$E' = H' / log2S$$

where S is the total number of species. E' is between 0 and 1.

Species richness and the Shannon-Wiener diversity and Pielou equitability indices were calculated with Past 4.09 (Palaeontological Statistics Software).

The Kruskal-Wallis test was used for the global comparison of the species richness and the Shannon-Wiener diversity and Pielou equitability indices of all the sites.

The unsupervised learning artificial neural network (self organizing map – SOM) method was used to order the study sites according to species assemblages using the fish population abundance database. The SOM method is recognized as a powerful tool for describing species distribution and fish assemblages (Lek et al. 2005) because it allows for the analysis of complex non-linear data (Kohonen 2001). The statistical protocol used is consistent with studies by Ibarra et al. (2005), Konan et al. (2006), and Lederoun et al. (2021).

An index of indicator value (IndVal) was calculated for each species according to Dufręne and Legendre (1997) to determine if the different typical communities identified by the SOM could be characterized by indicator species. Indicator species are defined as the species most characteristic of each group (species specificity) and found in the majority of the sites they characterize (species fidelity). In this study, we calculated an IndVal value for each group and at each level of the hierarchical classification from the SOM. IndVal values greater than 25% were considered significant because they implied that the species was present in at least 50% of the sites in the group and that the sites in this group contained at least 50% of the individuals of this species (Dufręne and Legendre 1997). The IndVal interface (version 2.0) was used for Windows to conduct this analysis.

Results

Fish community composition

During the study period, we cataloged a total of 58 species from 49 genera and 34 families across the Lake Nokoué and Porto-Novo Lagoon complex (Table 1). The most species-rich families were the Cichlidae, with six species (10.3%), followed by the Gobiidae with five species (8.6%), and both the Eleotridae and Carangidae families, each contributing four species (6.9%). The remaining families, which constituted 67.2% of the ichthyofauna, were represented by one or two species. In terms of distribution, 45 species were identified in Lake Nokoué, while 48 species were noted in the Porto-Novo Lagoon, with 35 species common to both water bodies. The ecological categorization within the complex revealed a diverse range of habitat affiliations: occasional continental forms and strict estuarine forms were the most prevalent, each comprising 20.7% of the species. This was followed by estuarine forms of marine origin (17.2%), marine-estuarine forms (15.5%), estuarine forms of continental origin (8.6%),

Table 1

Fish species collected at sampling sites and their occurrence in the Lake Nokoué and Porto-Novo Lagoon complex. Ce – continental forms with estuarine affinity; Co – occasional continental forms; Ea – ecological category; Ec – estuarine forms of continental origin; Em – estuarine forms of marine origin; Es – strict estuarine forms; F – occurrence (frequency); Ma – accessory marine forms; ME – marine-estuarine forms; Mo – occasional marine forms. 1 = presence of the species

Family and species	Porto-Novo Lagoon			Lake Nokoué			F (%)	Ea
	Agbokou	Djassin	Aguégués	Ganvié	Center of lake	Dantokpa		
Polyteridae (1)								
Polypterus senegalus Cuvier	1						16.7	Co
Elopidae (2)								
Elops lacerta Valenciennes	1	1	1		1	1	75.0	ME
Elops senegalensis Regan	1	1	1	1	1	1	66.7	Ma
Ophichthyidae (1)								
Dalophis boulengeri Blache et Bauchot					1		8.3	Es

Family and species	Porto-Novo Lagoon			Lake Nokoué			F (%)	Ea
	Agbokou	Djassin	Aguégués	Ganvié	Center of lake	Dantokpa		
Mormyridae (2)								
Brevimyrus niger (Günther)	1	1		1			16.7	Co
Hyperopisus bebe (Lacepède)		1					25.0	Co
Gymnarchidae (1)								
Gymnarchus niloticus Cuvier		1					8.3	Co
Clupeidae (2)								
Ethmalosa fimbriata (Bowdich)	1	1	1	1	1	1	100	Em
Pellonula leonensis Boulenger	1	1	1		1	1	75.0	Ec
Alestidae (2)								
Brycinus longipinnis (Günther)		1					25.0	Co
Hydrocynus forskali (Cuvier)	1						16.7	Co
Hepsetidae (1)								
Hepsetus odoe (Bloch)	1			1			41.7	Co
Mochokidae (2)								
Synodontis nigrita Valenciennes	1	1			1		41.7	Co
Synodontis ouemensis Musschoot & Lalèyè	1	1	1	1			33.3	Co
Schilbeidae (2)								
Parailia pellucida (Boulenger)	1	1	1			1	25.0	Ce
Schilbe intermedius Rüppell	1	1					33.3	Ce
Claroteidae (2)								
Chrysichthys nigrodigitatus (Lacepède)	1	1	1	1	1	1	100	Ec
Chrysichthys auratus (Geoffroy Saint-Hilaire)	1	1				1	83.3	Ec
Clariidae (1)								
Clarias ebriensis Pellegrin	1		1				8.3	Es
Eleotridae (4)								
Bostrychus africanus (Steindachner)	1		1	1	1		16.7	Es
Dormitator lebretonis (Steindachner)	1					1	41.7	Es
Eleotris senegalensis Steindachner	1	1				1	25.0	Es
Eleotris vittata Duméril	1	1	1	1		1	100	Em
Gobiidae (5)								
Awaous lateristriga Valenciennes	1						8.3	Es
Gobioides africanus (Giltay)		1				1	16.7	Es
Gobioides sagitta (Günther)		1				1	25.0	Es
Gobionellus occidentalis (Boulenger)	1	1	1	1	1	1	91.7	Es
Porogobius schlegelii (Günther)	1	1	1	1	1	1	91.7	Es
Mugilidae (2)								
Mugil cephalus Linnaeus	1	1	1	1	1	1	58.3	ME
Neochelon falcipinnis (Valenciennes)	1	1	1	1	1	1	58.3	Em
Cichlidae (6)								
Chromidotilapia guntheri (Sauvage)	1	1	1		1		41.7	Co
Coptodon guineensis (Günther)	1	1	1	1	1	1	100	Es
Coptodon mariae Boulenger	1	1		1	1		25.0	Ec
Hemichromis bimaculatus Gill	1	1		1			25.0	Co
Hemichromis fasciatus Peters	1	1	1	1	1		100	Ec
Sarotherodon melanotheron Rüppell	1	1	1	1	1	1	100	Es
Hemiramphidae (1)								

Family and species	Porto-Novo Lagoon			Lake Nokoué			F (%)	Ea
	Agbokou	Djassin	Aguégués	Ganvié	Center of lake	Dantokpa		
Hyporamphus picarti (Valenciennes)		1			1	1	41.7	Ma
Belonidae (1)								
Strongylura senegalensis (Valenciennes)	1				1	1	33.3	Em
Carangidae (4)								
Caranx crysos (Mitchill)					1	1	25.0	ME
Caranx hippos (L.)	1	1			1	1	75.0	ME
Lichia amia (L.)					1		8.3	Em
Trachinotus teraia Cuvier						1	16.7	Em
Sphyraenidae (1)								
Sphyraena guachancho Cuvier	1	1					50.0	ME
Anabantidae (1)								
Ctenopoma kingsleyae Günther	1						8.3	Co
Channidae (1)								
Parachanna obscura (Günther)	1	1	1				33.3	Ce
Paralichthyidae (1)								
Citharichthys stampflii (Steindachner)	1	1	1	1	1	1	83.3	Em
Soleidae (1)								
Solea solea (L.)						1	8.3	Ma
Cynoglossidae (1)								
Cynoglossus senegalensis (Kaup)	1	1	1		1	1	83.3	Em
Scombridae (1)								
Scomberomorus tritor (Cuvier)						1	25.0	Ma
Gerreidae (1)								
Eucinostomus melanopterus (Bleeker)	1	1	1	1	1	1	91.7	ME
Serranidae (1)								
Epinephelus aeneus (Geoffroy Saint-Hilaire)						1	25.0	ME
Monodactylidae (1)								
Monodactylus sebae (Cuvier)	1	1		1	1		58.3	Em
Haemulidae (1)								
Pomadasys jubelini (Cuvier)	1	1	1		1	1	100	Em
Polynemidae (1)								
Polydactylus quadrifilis (Cuvier)	1	1	1				58.3	ME
Lutjanidae (2)								
Lutjanus agennes Bleeker						1	16.7	Mo
Lutjanus goreensis (Valenciennes)				1	1	1	91.7	ME
Sciaenidae (1)								
Pseudotolithus senegalensis (Valenciennes)		1					8.3	Ma
Acanthuridae (1)								
Acanthurus moronviae (Steindachner)						1	50.0	Mo
Total	41	39	24	21	28	33		

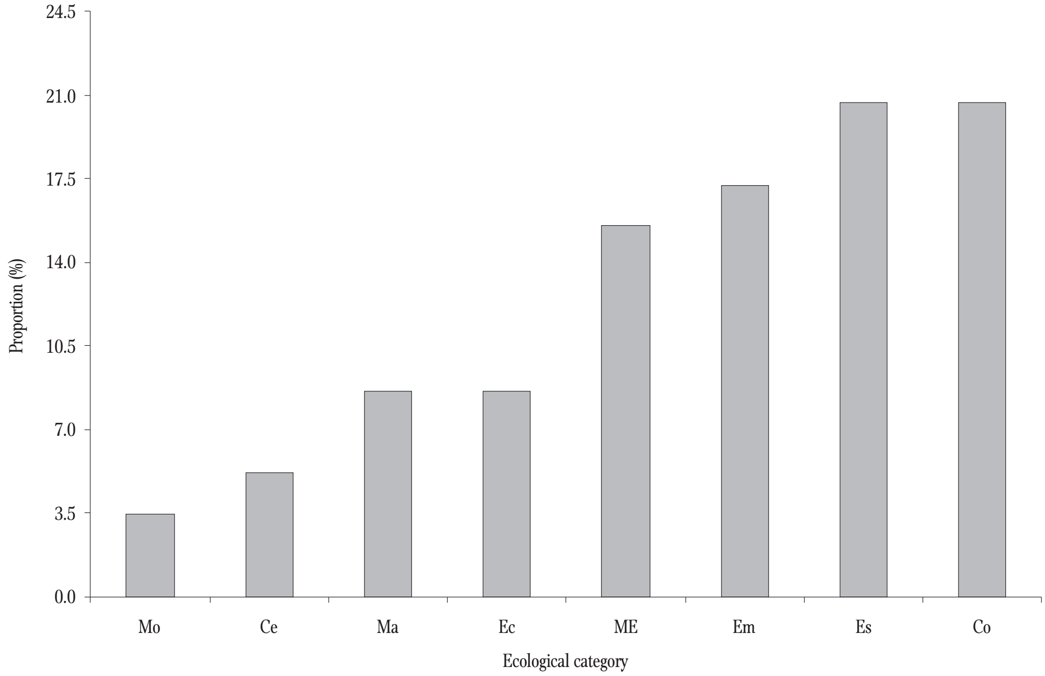


Figure 2. Classification of fish species by ecological category. Mo – occasional marine forms; Ce – continental forms with estuarine affinity; Ma – accessory marine forms; Ec – estuarine forms of continental origin; ME – marine-estuarine forms; Em – estuarine forms of marine origin; Es – strict estuarine forms; Co – occasional continental forms.

accessory marine forms (8.6%), continental forms with estuarine affinity (5.2%) and finally occasional marine forms (3.4%) (Fig. 2).

Occurrence and similarity among sites

The frequency of various fish species is given in Table 1. Constant and accessory species were the most common, constituting 37.9 and 36.2% of the fish fauna, respectively. Accidental species accounted for 25.9% of the species diversity. Notably, *Chrysischtys nigrodigitatus* (Geoffroy Saint-Hilaire), *C. guineensis*, *Eleotris vittata Duméril*, *Ethmalosa fimbriata* (Bowdich), *H. fasciatus*, *Pomadasys jubelini* (Cuvier), and *S. melanotheron* were identified as constant species, appearing in at least one survey at each site throughout the year.

An analysis of site comparison, using the Jaccard similarity index (Fig. 3) revealed notable patterns of similarity primarily among sites located in close geographically proximity. The highest degree of similarity (73.5%) was observed between Aguégués and Agbokou in the Porto-Novo Lagoon, while the lowest (40%) was between Dantokpa and Ganvié in Lake Nokoué, and Agbokou (Porto-Novo Lagoon) and Dantokpa (Lake Nokoué). These findings suggested the delineation of two distinct groups of sites (Fig. 3). The first included Dantokpa and the center of Lake Nokoué, positioned near the mouth, and the second

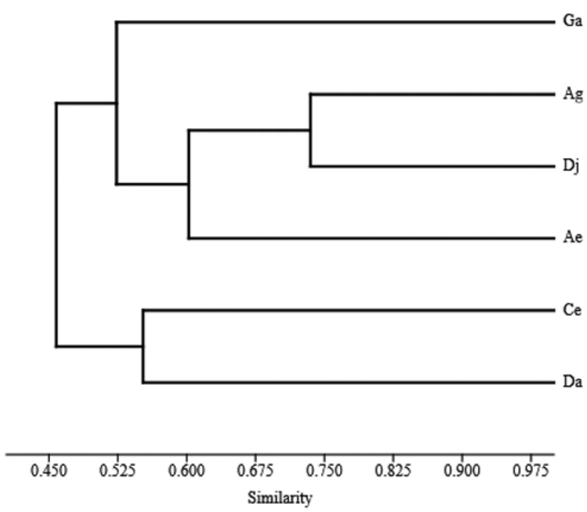


Figure 3. Dendrogram of the Hierarchical Ascending Classification of the surveys (matched group method coupled with the Jaccard similarity index). Ga – Ganvié; Ag – Agbokou; Dj – Djassin; Ae – Aguégués; Ce – center of Lake Nokoué; Da – Dantokpa.

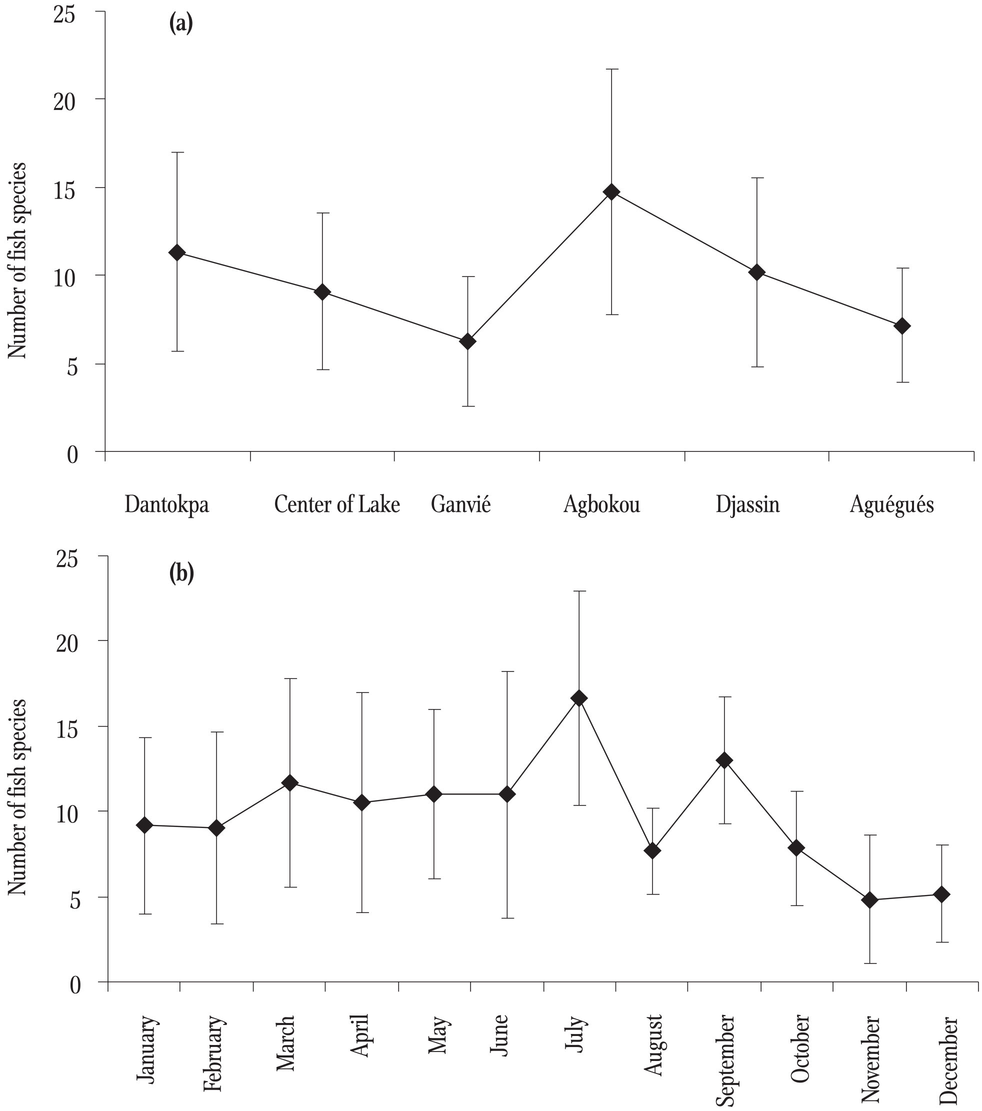


Figure 4. Spatial (a) and temporal (b) changes in species richness.

encompassed the remaining sites, which exhibited lesser similarity with the first group.

This distribution underscored the influence of geographical proximity and ecological conditions on species occurrence and diversity, highlighting the complex ecological dynamics within the Lake Nokoué and Porto-Novo Lagoon complex.

Spatial and temporal variations in species richness

Over the course of twelve monthly campaigns, species richness at each station ranged from an average of seven species in Ganvié to 15 species in Agbokou, (Fig. 4a). Monthly averages varied from five species in November to 17 species in July (Fig. 4b). Both site-specific and monthly variations in species richness were statistically significant (Kruskal-Wallis test, $P < 0.05$).

Temporal analysis revealed significant fluctuations in species richness throughout the year (Kruskal-Wallis test, $P < 0.05$), with a notable increase from 16 species in November to 38 in July, and an average of 27.2 ± 6.4 species.

Spatial and temporal variations of the Shannon diversity and Piélou equitability indices

The Shannon diversity index showed considerable variation, ranging from 0.89 (at Ganvié) to 1.94 (at Agbokou) (Fig. 5). When analyzing monthly data, the average Shannon diversity index varied from 0.97 in December to 1.77 in September (Fig. 6). The Kruskal-Wallis test revealed significant differences in Shannon diversity indices, both across different locations and over time ($P < 0.05$). Pielou equitability index also exhibited variation, with values ranging from 0.50 (at Ganvié) to 0.77 (at Djassin) (Fig. 5). Throughout the year, equitability ranged from 0.51 (in June) to 0.76 (in March) (Fig. 6). Similarly to the diversity index, significant differences in equitability were observed both spatially and temporally (Kruskal-Wallis test, $P < 0.05$).

Fish assemblage pattern and indicator species

The SOM procedure classified the sampling sites according to fish distributions and their occurrence probabilities. For this analysis, a 25-node map (5 rows x 5 columns) was chosen, exhibiting quantification errors of 1.188 and topography errors of 0.00, to project the sample data effectively. The outcomes of this analysis are illustrated in a dendrogram (Fig. 7). Each group shown on the map in Fig. 8 with the same pattern consisted of samples with similar taxonomic compositions.

Three main groups (I, IIa, and IIb) were identified. Group I included 75 and 50% of the samples from Dantokpa and the center of Lake Nokoué, while group IIb included 83.3 and 50% of the samples from Agbokou and Djassin on the Porto-Novo Lagoon, but three samples from Aguégués and two from Ganvié were found in this group. These two groups therefore included the samples from the four most extreme sites, i.e., Dantokpa and the center of Lake Nokoué, which are closer to the mouth, and Agbokou and Djassin, which are the farthest from the mouth. Group IIa mainly included samples from the intermediate sites, i.e., Ganvié and Aguégués.

Species distribution within the identified fish assemblages is presented in Fig. 9. Cluster I included 23 species, cluster IIa 25 species, and cluster IIb 10 species. The variation in species richness across

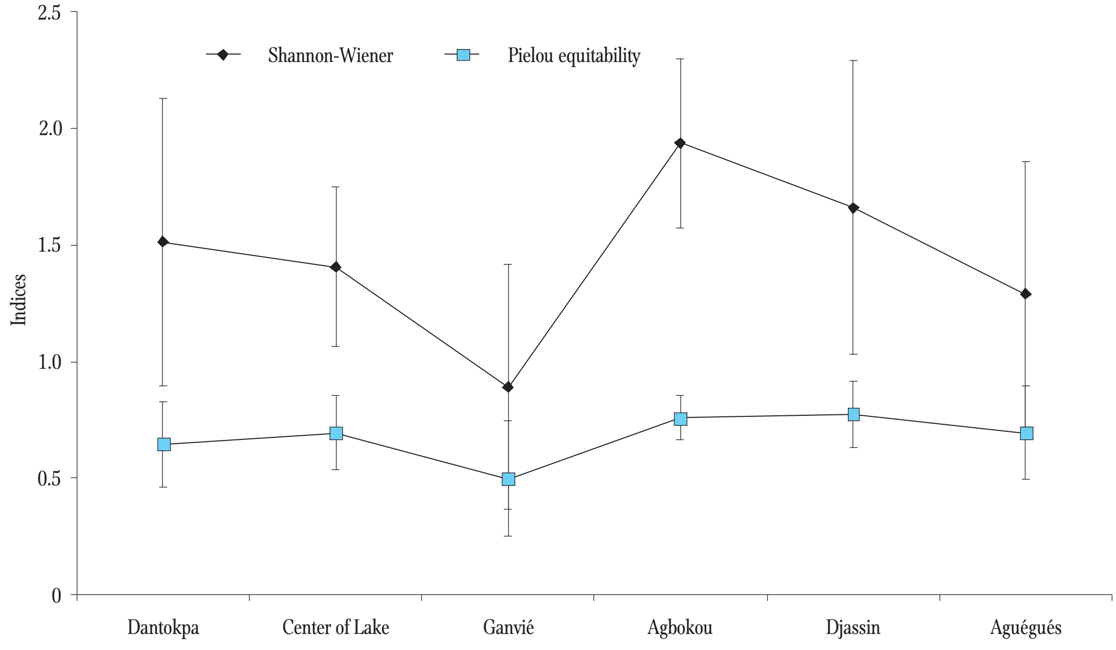


Figure 5. Spatial variations (average and standard deviation) in the Shannon-Wiener diversity and Pielou equitability indices.

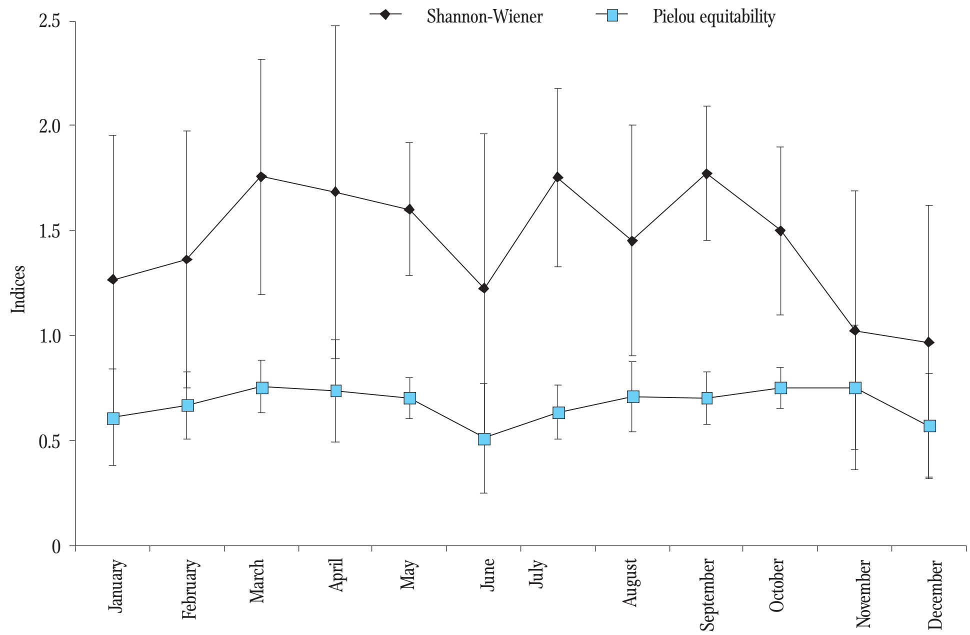


Figure 6. Temporal variations (average and standard deviation) in the Shannon-Wiener diversity and Pielou equitability indices.

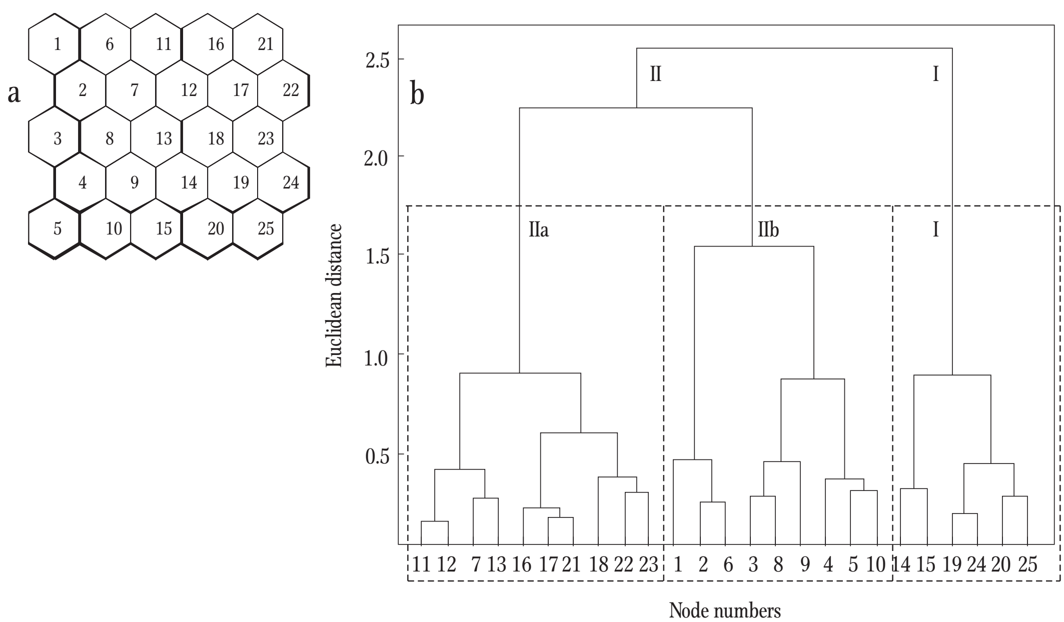


Figure 7. Hierarchical classification of the nodes of the Kohonen map based on the species richness of the sites (n = 6). a – self-organizing map (SOM) (25 nodes); b – hierarchical clustering of SOM nodes with the Ward linkage method and Euclidean distance: the numbers from 1 to 25 correspond to those assigned on each node of the SOM.

these groups is illustrated in Fig. 10. The differences in species richness were statistically significant between cluster IIb and both clusters I and IIa (Kruskal-Wallis test, $P < 0.05$).

The IndVal method facilitated the identification of distinct indicator species for each hierarchical level of the assemblage (Fig. 11). Within the first group, associated with Dantokpa and the center of Lake Nokoué, 15 species, representing 25.9% of the total specific richness, were identified as indicator species.

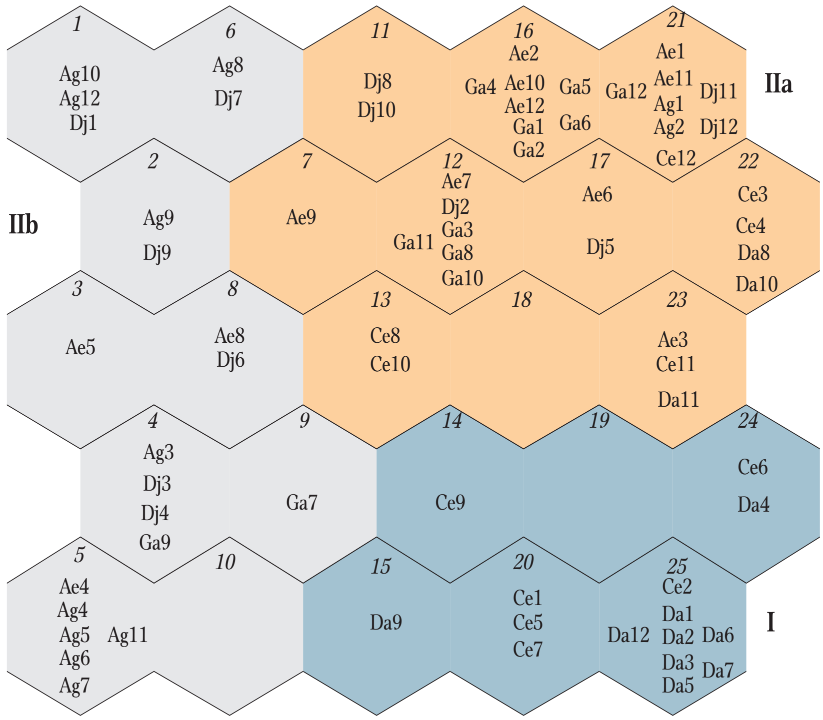
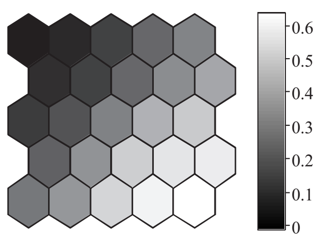
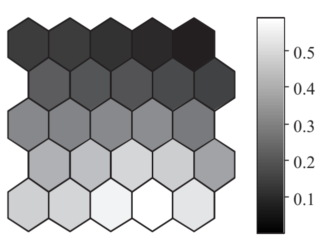


Figure 8. Classification of samples using occurrence data through the learning process of the self-organizing map. The defined clusters are numbered I, IIa, and IIb. Ae (Aguégués), Ag (Agbokou), Ce (center of Lake Nokoué), Da (Dantokpa), Dj (Djassin), and Ga (Ganvié) are the sites codes. Numbers 1 through 12 match the samples. Numbers 1 through 25 in the corner represent the node numbers.



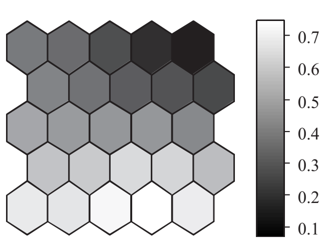
Cluster I

Acanthurus moroviae, *Caranx crysos*, *C. hippos*, *Citharichthys stampfilii*, *Dalophis boulengeri* , *Elops lacerta*, *Epinephelus aenus*, *Ethmalosa fimbriata*, *Eucinotonus melanopterus*, *Gobioides africanus*, *G. sagitta*, *Gobionellus occidentalis*, *Hyporamphus picarti*, *Lichia amia*, *Neochelon falcipinnis*, *Lujanus agennes*, *L. goreensis*, *Mugil cephalus*, *Pomadasys jubelini*, *Scomberomorus tritor*, *Solea solea*, *Strongulura senegalensis*, *Trachinotus teraia*.



Cluster IIa

Awaouss lateristriga, *Brevimyrus niger*, *Brycinus longipinnus*, *Chromidotilapia guntheri*, *Chrysichthys auratus*, *C. nigrodigitatus*, *Coptodon mariae*, *Ctenopoma kingsleyae*, *Cynoglossus senegalensis*, *Domitator lebretonis*, *Eleotris senegalensis*, *E. vittata*, *Gymnarchus niloticus*, *Hemichromis bimaculatus*, *Heseptus odoe*, *Hyperopisus bebe*, *Monodactylus sebae*, *Parachanna obscura*, *Polydactylus quadrifilis*, *Polypterus senegalensis*, *Pseudotolithus senegalensis*, *Schilbe intermedius*, *Sphyraena guanchancho*, *Synodontis nigrita*, *Synodontis ouemensis*.



Cluster IIb

Bostrychus africanus, *Clarias ebriensis*, *Coptodon guineensis*, *Elops senegalensis* , *Hemichromis fasciatus*, *Hydrocynus forskali*, *Parallelia pellucida*, *Pellonulla leonensis* , *Porogobius schlegelii*, *Sarotherodon melanotheron*.

Figure 9. Fish species distribution patterns in each cluster are defined by the hierarchical clustering applied to the self-organizing map units. Dark color represents a high probability of occurrence, and light color indicates a lower probability.

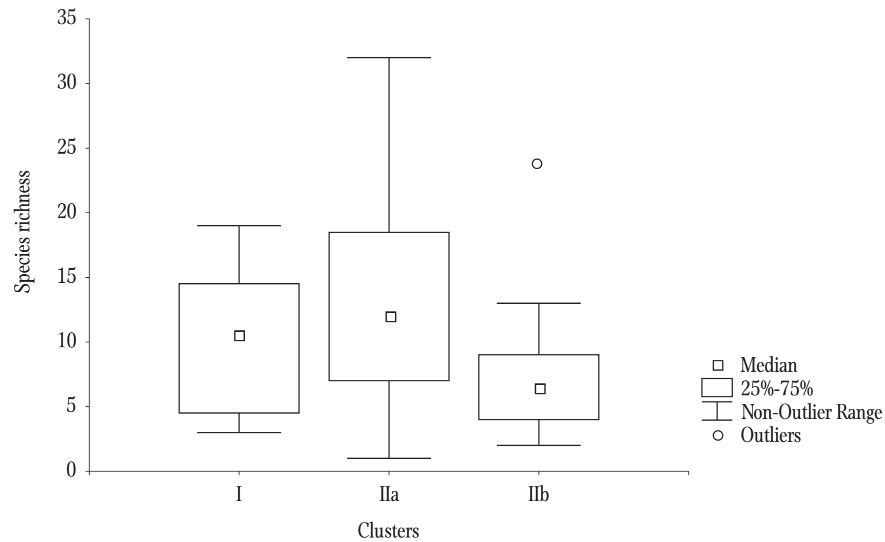


Figure 10. Boxplot comparing fish species richness in the three clusters defined by the self-organizing map.

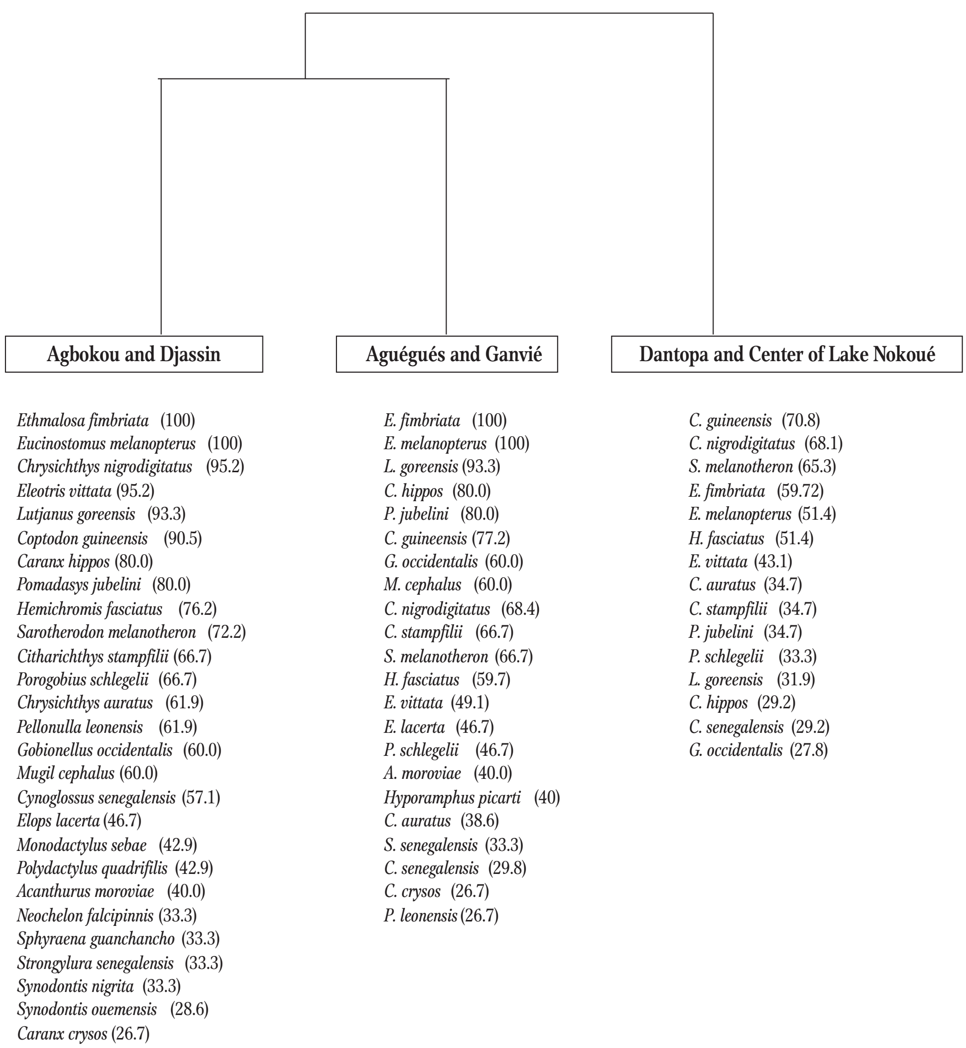


Figure 11. Indicator species for each cluster of the dendrogram resulting from the self-organizing map procedure (n = 6). IndVal values (in %) are shown in brackets. Indicator values (P < 0.05) are only those greater than 25%.

At the second level, corresponding to Aguégués and Ganvié, 22 species emerged as indicators. The third group, predominantly comprising Agbokou and Djassin, was characterized by 27 indicator species.

Discussion

This study aimed to update knowledge of the spatio-temporal distribution of ichthyofauna within the Lake Nokoué and Porto-Novo Lagoon complex, integral to Ramsar site 1017, in south Benin. Using gillnets of various mesh sizes permitted collecting comparable data across different sites (Lederoun et al. 2021). Our comprehensive survey identified 58 species across 49 genera and 34 families within the complex. This diversity highlights the importance of the complex as a habitat for a wide range of fish species, reflecting a rich mosaic of ecological niches and interactions between marine and freshwater environments.

Historical data illustrate the fluctuations in fish species richness in Lake Nokoué over the past 40 years. Gras (1961) reported 87 species belonging to 43 families, while Lalèyè (1995) identified 78 species belonging to 36 families. In the late 1990s, Adité and Winemiller (1997) recorded 35 species belonging to 20 families in the lake, while Lalèyè and Philippart (1997) reported a higher species richness of 67 species belonging to 33 families. Niyonkuru (2001) and Lalèyè et al. (2003) recorded 51 species belonging to 33 families. Our study, which documented 45 species in Lake Nokoué and 48 in Porto-Novo Lagoon, did not necessarily indicate a decline in species richness. The discrepancy between our results and previous ones could be attributed to different methodologies, including study duration and fishing techniques used (Lalèyè et al. 2003). It is obvious that species richness could increase by combining various fishing methods and by exploiting data from literature and collections in natural history museums (Lederoun et al. 2018). A more diverse application of fishing methods combined with an analysis of historical data and museum collections could reveal richer biodiversity (Lederoun et al. 2018). Recent research using data from collections at the Directorate of Fisheries Production of Benin and the literature up to 2023, identified 110 native species and one introduced species, encompassing 87 genera and 51 families in Lake Nokoué alone (Lederoun, pers. comm.). This high biodiversity was partly obscured by the limited exploration of acadjas (a type of fish park composed either of branches stuck in the bottom of water or of floating vegetation) during this study (Lederoun et al. 2020). A more thorough investigation of these habitats could potentially increase the documented number of species because acadjas offer critical refuge, breeding grounds, and feeding areas conducive to fish survival and reproduction.

Among the sites examined at Lake Nokoué, species richness varied significantly, with the lowest observed at Ganvié and the highest at Dantokpa. The diminished diversity at Ganvié can largely be attributed to pronounced anthropogenic impacts. Conversely, the presence of many marine species in Dantokpa, including both juveniles and adults, was linked to the site's salinity-owing to its proximity to the mouth of the lake-and its role as a nursery habitat, a function supported by numerous studies (Dorr et al. 1985, Albaret 1994, Diouf 1996, Vidy 2000, Niyonkuru 2001, Vidy et al. 2004). Additionally, the depth of the lake plays a crucial role in determining species richness at Dantokpa, making it a primary factor influencing lake ichthyofauna (Hugueny 1990, Paugy and Bénèch 1989). Depth measurements during our study confirmed that Dantokpa was the deepest site (3.5 ± 0.52 m), and depths ranged considerably among locations. The average depths were 0.51 ± 0.09, 0.75 ± 0.15, 1.1 ± 0.20, 1.5 ± 0.43 and 2.01 ± 0.62 m for Ganvié, Aguégués, Djassin, and the center of Lake Nokoué and Agbokou, respectively.

In the Porto-Novo Lagoon, our study identified 48 species of the 41 genera and 27 families, surpassing previous counts by Yacoubou (2005) and Lederoun (2006). Species richness was notably high in Agbokou and Aguégués, the latter influenced by the dense concentration of acadjas that provide refuge and increase fish productivity. Unlike Aguégués, Agbokou had fewer acadjas, which were not investigated during this study, potentially affecting the diversity obtained. Moreover, aquatic vegetation at Agbokou, which supports a rich array of benthic macroinvertebrates, likely contributed to the species richness observed. The diversity of habitats in the Porto-Novo Lagoon explained the variation in species richness compared to that in Lake Nokoué. Habitat diversity impacts biotic interactions and essential life functions such as reproduction, feeding, and shelter, reducing interspecies competition and fostering biodiversity conservation. Additionally, the proximity of Agbokou to the Ouémé River, bringing a significant influx of freshwater species, further accounts for the site's high species richness.

Diversity indices play a crucial role in evaluating the health of aquatic ecosystems, although they may not fully capture the organizational structure of fish communities within these environments (Lobry et al. 2003). In the Lake Nokoué and Porto-Novo Lagoon complex, both the diversity and uniformity of fish communities were found to be relatively low. A diversity index below 2 indicates a notable environmental imbalance or degradation (Khalaf et al. 2009). This phenomenon can be attributed largely to the uneven distribution of fish species, with a pronounced dominance of certain species such as *C. guinnensis*, *C. nigrodigitatus*, *E. fimbriata*, *Eucinostomus melanopterus* (Bleeker), *Gobionellus occidentalis* (Boulenger), *Lutjanus goreensis* (Val.), *Pellonulla leonensis* Boulenger, *Porogobius schlegelii* (Günther), and *S. melanotheron*, which vary greatly from one site to another.

Artificial neural networks (ANNs), particularly Kohonen self-organizing maps (SOM), were employed in this study to address the classification and ordination challenges inherent in ecological data. SOMs, an unsupervised learning method, are preferred over traditional methods like PCA for their efficacy in handling data extremes—be it high abundance or rarity (Brosse et al. 2001, Giraudel and Lek 2001, Villanueva 2004). Kohonen's self-organizing maps (Kohonen 2001) have been applied in various fields ranging from engineering to chemistry (Blasco et al. 2000), from remote sensing (Aurelle et al. 1999, Foody and Cutler 2003) to economics and water quality monitoring (Walley et al. 2000, Aguilera et al. 2001). In ecology, SOMs have been used in the classification of benthic diatom communities (Gosselain et al. 2005, Tison et al. 2005, Park et al. 2006), benthic macroinvertebrates (Compin et al. 2005, Park et al. 2003a, 2003b, 2005, 2006), and fishes (Ibarra et al. 2005, Park et al. 2005, Penczak et al. 2005, Lederoun et al. 2021). The SOM analysis in this study delineated three distinct sites groups based on monthly species abundance data, a pattern seemingly influenced by salinity gradients across the sites. Indeed, Dantokpa and the center of Lake Nokoué are closer to the mouth and are colonized by marine and estuarine species, and Ganvié and Aguégués are the closest to the Ouémé River and are colonized by continental species. Djassin and Agbokou are intermediate with a mixture of the different communities observed. It is widely recognized that many interacting physical and biological factors influence the presence, distribution, abundance, and diversity of estuarine tropical fishes (Whitfield 1998, Blaber 2000) and water salinity is often cited as a determinant of fish ecology in these lagoon environments (Whitfield 1998, Albaret 1999, Blaber 2000).

Conclusion

This study updates the knowledge about the spatial and temporal dynamics of ichthyofauna in the Lake Nokoué and Porto-Novo Lagoon complex. Through extensive surveys, we cataloged 58 species belonging to 49 genera and 34 families. These were predominantly estuarine and marine species. Notably, the Agbokou and Djassin sites in the Porto-Novo Lagoon emerged as biodiversity hotspots, hosting 44 and 41 species, respectively, representing 75.9% and 70.7% of the total fish fauna identified. The classification of sites into three main groups based on their proximity to the mouth of the lake and the Ouémé River, the principal source of fresh water in the complex, revealed distinct fish assemblages, each characterized by unique indicator species. These findings underscore the need for focused conservation efforts to safeguard the ichthyofauna of this vital ecosystem.

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